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A New Miocene Molossid Bat from La Venta, Colombia, South America

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Abstract

A new genus and species of fossil molossid bat, *Kiotomops lopezi*, from the Middle Miocene La Venta fauna in Colombia, is described. In South America only two other Tertiary bats have been discovered: *Notonycteris magdalenensis* and *Mormopterus faustoi*. The former, known only from its lower dentition, is classified in the Phyllostomidae; the latter, in the Molossidae, by its upper molar morphology. *Kiotomops lopezi* is established based on an upper molar showing molossid affinity but is clearly different from *Mormopterus* in the absence of hypocone. It is closely related to *Molossus* and its allies.

The upper molar of *Kiotomops* shows typical dilambdodonty and has three noticeable characteristic features; (1) lack of hypocone and basal-cingulum, (2) presence of a conical parastyle and trigonal pyramid-like "stylocone-like lobe", and (3) having a posteriorly situated mesostyle. Although the phylogenetic relations among the genera within the family Molossidae are not well understood, we regard *Kiotomops* as a specialized side branch, closely related to the genus *Molossus*.

1. Introduction

The La Venta fauna (STIRTON, 1951) is one of the most famous and richest Neogene vertebrate faunas known in northern South America; it is assigned to the Friasian Land Mammal Age of South America, dating about 14 Ma and corresponding to the Middle Miocene (MARSHALL *et al.*, 1977; HAYASHIDA, 1984; SETOGUCHI & ROSENBERGER, 1985; TAKEMURA & DANHARA, 1986). Many medium- to large-sized land mammals have been found in La Venta but only a few small-sized mammals have been discovered. Recently, many small mammalian teeth have been discovered by the washing and screening method at the Kyoto Site, within the Monkey Unit of the Honda Formation along the Magdalena River, Colombia (SETOGUCHI, 1985; SETOGUCHI & ROSENBERGER, 1985). Two isolated upper molars of a molossid bat were found associated with these recent discoveries.

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These are described below.

From La Venta, the only chiropteran fossil, *Notonycteris magdalenensis* has been described based on three incomplete lower jaws with M_1 and/or M_2 and several fragments of limb bones; it has been identified as a member of the Phyllostomidae (SAVAGE, 1951). As the present, the new chiropteran material is comprised of isolated upper molars, making direct comparison with *Notonycteris* impossible. It is clear, however, that the present form showing the molossid affinity does not share the same family as *Notonycteris* because *Notonycteris* lacks the specialization seen in the molossid lower dentition.

Beside the La Venta specimen, another South American Tertiary bat has been discovered in Brazil: *Mormopterus* (*Neomops*) *faustoi*, originally described as *Tadarida faustoi* PAULA COUTO, but regarded as a species of *Mormopterus* by comparison with living and European fossil molossids (LEGENDRE, 1984b). The deposit in which it was discovered was originally thought to be of the Pleistocene, but it has been re-dated to the Early to Late Oligocene (PAULA COUTO & MEZZALIRA, 1971), or to the Late Oligocene to the Early Miocene (MCKENNA, 1980). Whichever the case, it represents the earliest record of fossil bats occurring in South America.

A detailed comparison of the present form with *Mormopterus* is given. Phylogenetic reconstruction of the family Molossidae is attempted.

2. Systematic Accounts

Order Chiroptera BLUMENBACH, 1779
Suborder Microchiroptera DOBSON, 1875
Infraorder Vespertilionia VAN VALEN, 1979
Family Molossidae GERVAIS, 1855
Subfamily Molossinae LEGENDRE, 1984

Kiotomops, new genus

Type species: *Kiotomops lopezi*, new species.

Including species: Type species only.

Locality and age: The "Kyoto Site" near La Venta, within the Monkey Unit of the Honda Formation, Huila Department, Colombia, South America; Middle Miocene, approximately 14 million years old (MARSHALL *et al.*, 1977; HAYASHIDA, 1984; TAKEMURA & DANHARA, 1986).

Etymology: "Kioto" after the Kyoto Site (el sitio de Kioto, in Spanish) where the type specimen was discovered, and "mops", meaning molossid bat.

Diagnosis: The vertical notch between the paracone and metacone is very deep, and reaches to the labial edge of the crown. The trigonal pyramid-like stylar cusp B is prominently high and is connected with the paracone by the preparacrista. The mesostyle is posterior to the vertical notch. Between the stylar cusp B and the mesostyle is a

deep labial groove touching the vertical notch. Neither basal cingulum nor hypocone is present.

Kiotomops lopezi, new species
(Fig. 1)

Holotype: Left M^1, IGM-KU 82C1, deposited in Instituto Nacional de Investigaciones Geológico-Mineras (INGEOMINAS), Bogotá, Colombia.

Hypodigm: Right M^2(?), IGM-KU 82C2, deposited in the same institute as the holotype.

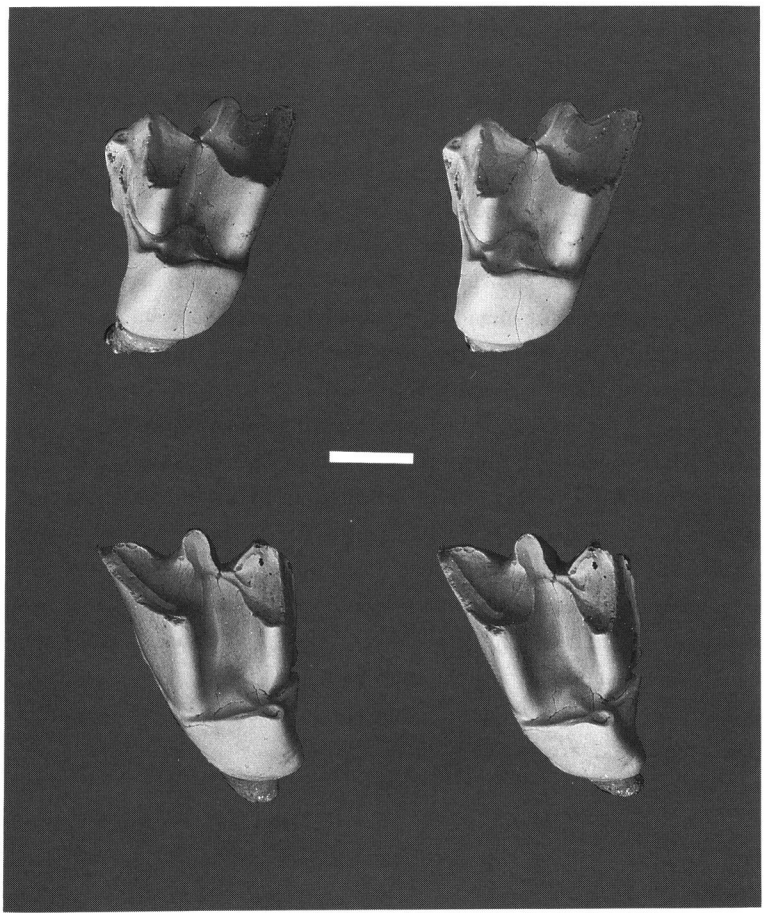

Fig. 1. *Kiotomops lopezi*, new genus and species (stereo pairs). Top pair: left M^1, IGM-KU 82C1; bottom pair: right M^2, IGM-KU 82C2. Scale: 1 mm.

Etymology: *lopezi*, after Dr. Alfonso LOPEZ REINA, the former director of INGEOMINAS.

Diagnosis: As for genus.

Description: The occlusal view is almost squared. The molar is tri-cusped and without hypocone. As the metacone is higher and larger than the paracone, the paracone is situated more labially with respect to the metacone. The vertical notch between the paracone and metacone is very deep. This dilambdodont condition is more distinct than in didelphoid molars. On the holotype, IGM-KU 82C1, the protocone is crescent and situated so closely to the paracone that the trigon basin is very narrow and the postprotocrista runs almost posteriorly.

On the narrow stylar area, four stylar cusps are observed; parastyle, stylar cusp B, mesostyle, and metastyle. (The homology of the stylar cusp B is mentioned in the discussion.) The parastyle is conical and connected with the protocone by the paracingulum-preprotocrista and with the stylar cusp B by a short ridge. The trigonal pyramid-like stylar cusp B, which is higher and slightly more protruded labially than the parastyle, is connected with the paracone by the preparacrista. The mesostyle is situated far posteriorly to the vertical notch between the paracone and metacone. The labial groove between the stylar cusp B and mesostyle is deeply excavated lingually and reaches very closely to the vertical notch so that these four ridges join together, making a X-shaped configuration. The metastyle protrudes postero-labially, and is not connected with the protocone by the postprotocrista-metacingulum, which disappears half way of the posterior face of the metacone. These four stylar cusps are connected by a waving ridge.

The basal cingulum and the hypocone are not present at all.

The molar is three rooted: one is beneath the protocone and the other two are beneath the labial side of the crown. The lingual root is the most robust.

The other material, IGM-KU 82C2, identified as M^2 of the same species, shares the common features with IGM-KU 82C1 except for the following morphology seen in the former; (1) a conical protocone, (2) an occlusal outline protruding posterolabially, (3) a labial groove is present between the mesostyle and metastyle, and (4) a paracone is not so much reduced as the metacone unlike IGM-KU 82C1. Because of the larger paracone, IGM-KU 82C2 is assigned to M^2 rather than M^1.

The molar size is almost equal to general molossid bats. Crown dimensions of IGM-KU 82C1 and 82C2 are as follows:

	IGM-KU 82C1	IGM-KU 82C2	
length	2.2	(2.1)*	
width**	3.1	3.1	(mm)

* The anterolabial corner is broken.

** The transverse length is between the top of the mesostyle and the base of the protocone.

3. Discussion

Kiotomops shows typical dilambdodonty and has no hypocone. The same morphology is also seen in the Didelphidae (Marsupialia), Talpidae (Insectivora), Chiroptera and Tupaiidae (Scandentia). Neither fossil nor living talpids and tupaiids have ever been recorded in South America as yet. The present form must be classified either as a marsupial, or, most probably, a bat.

Of all South American marsupials, only didelphids have the typical dilambdodont dentition. Although many morphological similarities of the dentition are seen between didelphids and chiropterans without hypocone, didelphid molars are characterized by the following features; a widely developed stylar shelf, the retention of the stylocone and four other stylar cusps, relatively shallow vertical notch between the paracone and metacone situated far lingually from the labial border of the crown, a relatively conical and low paracone and metacone, and a nearly triangular outline of the crown. None of these features are observed on IGM-KU 82C1 except for the presence of the stylar cusp B on the same position as the stylocone in the didelphids. It is safe to conclude that the present form is regarded as a member of the Order Chiroptera rather than of the Marsupialia.

Living bats are classified into two suborders; Old World Megachiroptera, with bunodont molars suitable for a frugivorous or nectivorous dietary specialization, and the Microchiroptera. The present form is clearly not a member of the first suborder. The second suborder is classified into two infraorders (Van Valen, 1979); the Phyllostomatia, with distinct hypocones on their molars, and the Vespertilionia, mostly adapted to insectivory.

A complete basal cingulum is present on anterior upper molars in the Vespertilionidae and Thyropteridae. The Thyropteridae have a distinct postmetaconulecrista and a hypocone surrounded by the basal cingulum. In the other families, however, the basal cingulum is incompletely preserved at the lingual base of the crown.

Although the remaining vespertilionian families (Natalidae, Furipteridae and Molossidae) are easily distinguished from one another by the size and the dental formula, the anterior upper molar structure is similar in the three families. The common features of these three groups are the absence of the hypocone (with the exception of the Tadaridinae, member of the Molossidae), postmetaconulecrista and conules, and the presence of the vestigial basal lingual cingulum, which are also seen in *Kiotomops*. The natalids and furipterids share three common features which are not observed in molossids (except for the Tadaridinae). The first and most important feature is the presence of deep labial grooves anterior and posterior to the mesostyle. The grooves are so deep as to reach to the paracone and metacone, and divide the stylar shelf into three narrow shelves. On the other hand, the labial grooves of the present form and the molossids are not so deep. Although the anterior groove of the present form is situated posteriorly, touching the

vertical notch between the paracone and metacone, the distinct labial edge is present on IGM-KU 82C1. (The rather deep posterior groove on IGM-KU 82C2 will be mentioned later.) The second is the presence of lophs. The natalids and furipterids have a small but distinct paraloph and metaloph. The present form does not have lophs either, and the molossids have no paraloph but retain a vestigial metaloph. The third one is the presence of the basal cingulum. As mentioned above, *Molossus* has no basal cingulum as well as the present form. By these facts, together with the vast distribution of present-day molossids over the world and the occurrence of molossid fossils from the Late Eocene in Europe, it is safe to conclude that *Kiotomops* is more closely related to the Molossidae, than to the Natalidae or Furipteridae.

Among the Molossidae, *Kiotomops* shares only with *Molossus* the following features on M^1 and M^2; (1) a hypocone or basal lingual cingulum absent, (2) posteriorly descending crest from the "metaconule" (=postmetaconulecrista) absent, and (3) neither paraloph nor metaloph so much developed, (4) paraconule or metaconule absent.

LEGENDRE (1982, 1984a, b, c) has recently reviewed the Molossidae taxonomically, including fossil species, mainly based on the dental formula and the morphology of the molars. He classified the Molossidae into three subfamilies (Molossinae, Cheiromelinae and Tadaridinae) and concluded that having diverged from the Eochiroptera during the Early Eocene, the molossids acquired a hypocone and then within some groups, the hypocone was reduced or disappeared (e.g. in *Molossus, Myopterus* and *Cheiromeles*). He re-examined the fossil materials from the Late Eocene in Montmartre, France, and established a new genus *Cuvierimops,* possessing a distinct hypocone, as an intermediate group between the primitive and the advanced molossids (LEGENDRE & SIGÉ, 1984; LEGENDRE, 1985). He hypothesized that the Late Eocene *Cuvierimops* lost its hypocone together with the lingual cingulum in the anterior molars and gave rise to the "*Molossus* group", which includes *Molossus, Myopterus*, and *Cheiromeles*. LEGENDRE & SIGÉ (1984) also suggested the possibility that some primitive species without a hypocone may have persisted as long as the emergence of the "*Molossus* group".

Kiotomops supports the latter hypothesis, because it has neither hypocone nor basal cingulum and it is thought to be closely related to *Molossus*. It is probably incorrect to hypothesize that the primitive molossids like *Cuvierimops*, with well developed hypocones, gave rise to the "*Molossus* group". Rather, it is more reasonable to hypothesize that the Molossidae, which branched off from the Eochiroptera during the Early Eocene, diverged into two major groups, one with a hypocone and the other without; this was probably before the incipient molossids had acquired a complete hypocone. This hypothesis is based on the diphyletic interpretation on the origin of the Molossidae, though the Molossidae have usually been treated as a monophyletic family. This is due to the facts that this hypothesis is based on solely upper anterior molar morphology and the homology of a hypocone on the molossid molars is still not clear.

4. Unique Morphology of the Stylar Cusps

Kiotomops is not regarded as the direct ancestor to the extant "*Molossus* group" because of its unique stylar-cusps morphology, which is not seen in chiropterans. This is the major reason why the present form represents a separate new genus, *Kiotomops*. The presence of the stylar cusp B on the holotype, IGM-KU 82C1, at the analogous position of the stylocone in primitive metatherian-eutherian grade mammals is worth mentioning. It is generally recognized that by early Cenozoic time, eutherians had already lost the original stylocone; the presence or the absence of the stylocone is one of the criteria when separating metatherian from eutherian upper molars (CLEMENS, 1979). If the stylar cusp B of IGM-KU 82C1 is to be identified as a true stylocone, *Kiotomops* must be treated as a member of the metatherians.

The metatherian-like features seen in *Kiotomops* are the presence of "stylocone", the position of the mesostyle and the absence of the hypocone. The third feature is not only seen in the metatherians but also in the tupaiids and talpids, and the second feature may be interpreted as specialization. As for the first, all vespertilionian upper molars do not have a stylar cusp B, or a conule-like "stylocone". Here, two interpretations may be probable; first, the stylar cusp B of *Kiotomops* is not a true stylocone but merely a topological upheaval on the preparacrista, and second, the stylar cusp B is a true stylocone and hence *Kiotomops* should be regarded as a marsupial (didelphid). As already mentioned above, both IGM-KU 82C1 and 82C2 have several eutherian morphological characteristics (e.g. narrow stylar shelf, deep vertical notch between the paracone and metacone, sharp crescent cones and relatively quadrate outline); topologically, the cusp is not independent but merely forms an upheaval at the junction of the preparacrista and the labial edge. All these features support the first interpretation that the stylar cusp B is not a true stylocone; *Kiotomops* must thus be regarded as an eutherian mammal. However, further discovery of the molarized P^3 or the presence of M^4 may confirm the second interpretation.

The unique morphology of the mesostyle of *Kiotomops*, which is situated excessively posterior to the vertical notch between the paracone and metacone is also worth discussing. Such position is hardly seen on vespertilionian upper molars, of which mesostyle is generally just labial to the vertical notch. On both IGM-KU 82C1 and 82C2, the mesostyle is dislocated very posteriorly, and hence the labial edge touches the vertical notch just anterior to the mesostyle. On IGM-KU 82C2, posterior to the mesostyle, there is a labial groove which is cutting off the labial edge of the crown, contrary to the shallow groove in IGM-KU 82C1. The topological difference seen in the posterior labial grooves between IGM-KU 82C1 and 82C2 may rather be regarded as intra-specific variation, since the remaining morphology between both specimens is very similar.

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